THE REPRODUCTION AND EARLY LIFE HISTORY OF THE GASTROPOD *BEMBICIUM NANUM* (LAMARCK, 1822) (FAM. LITTORINIDAE).

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(Plate viii; five Text-figures.)

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Synopsis.

Spawning in *B. nanum* takes place during the spring and summer. Eggs are laid in gelatinous egg masses attached to the rock surface and hatch after about 12 days as pelagic planktotrophic veligers. The relationship between habitat and breeding in New South Wales littorinids is similar to that of littorinid species in other parts of the world.

Introduction.

It is well known (Anderson, 1960) that the littorinids present an intriguing problem of development, some species of the mid- and upper reaches of the shore lacking a free-swimming stage (e.g., *Littorina obtusata*, *L. saxatilis*, Pelseneer, 1911; Delsman, 1914; Linke, 1934; Thorson, 1946), others of similar habitat retaining planktotrophic veligers (e.g., *L. neritoides*, Lebour, 1935; *L. angulifera*, Lebour, 1945). The marked zonation of the New South Wales rock-platform littorinids *Bembicium nanum* (Lamarck), *Melaraphe unifasciata* (Gray) and *Nodilittorina pyramidalis* (Quoy and Gaimard) raises the question, whether corresponding anomalies exist among these species. A partial answer can now be given on the basis of the present study of the reproduction and life history of *B. nanum*.

Spawning.

Observations during 1960 and 1961 on the breeding season and spawning of a population of *B. nanum* inhabiting the rock platform at Harbord, north of Sydney, showed that both males and females contained ripening gametes by the beginning of September, but the first egg masses were not found in this locality until the end of October. Thereafter, however, they were commonly found until the end of April. No female of *B. nanum* was observed in the act of spawning, but the egg masses of the species were identifiable on the more indirect criteria of correlation between the onset of seasonal sexual ripening and the occurrence of egg masses in the habitat, and of exact correspondence of dimensions and colour of ovarian eggs transferred to seawater and eggs in the egg masses. The occasionally observed close association of females with newly deposited egg masses also supported the identification.

Egg masses of various ages were maintained in dishes of aerated seawater and observed at frequent intervals and drawings of living embryos made using a camera lucida.

The photographs of Plate viii were taken by the Department of Medical Artistry, University of Sydney.

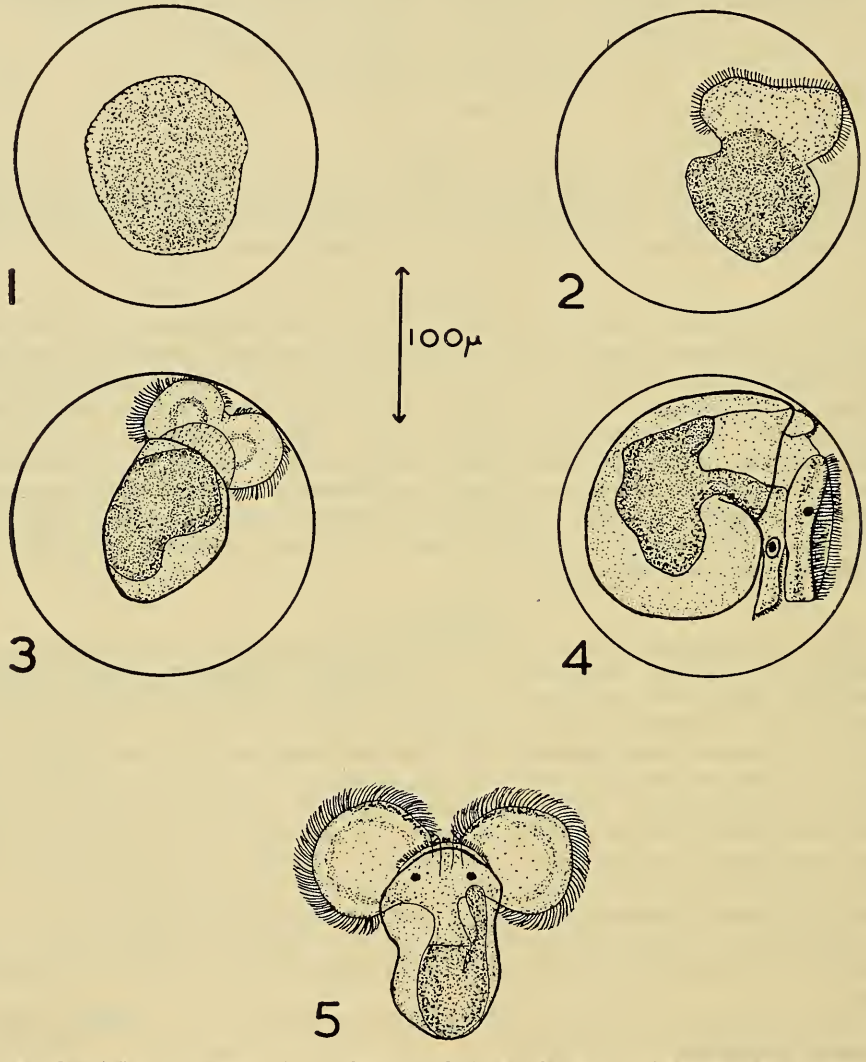
Development.

The spawn (Pl. viii) consists of an irregularly distributed, closely packed series of oval transparent jelly masses each containing about 100–200 creamy-white eggs 100μ in diameter, surrounded by ovoid transparent envelopes 200–220μ in length and 190–210μ in width. The group of jelly masses is firmly attached to the rock surface, generally in a sheltered position either in a fissure or under weed, in the habitat occupied by the adults.

The eggs develop rapidly, passing in about two days through a simple yolky trochophore stage (Text-fig. 1), then gaining in the succeeding two days the apical

tuft, blunt transverse foot and lateral velar lobes of the young veliger (Text-fig. 2). Rotation within the envelope begins at about this time.

During the next five days, the veliger enlarges and becomes more elaborate, with a well-developed bilobed velum and a pair of black eyespots, a ciliated foot with paired otocysts and thin operculum and a visceral hump covered by a shell in which the



Text-figs 1-5.—*B. nanum*. 1. Trochophore, 2 days. 2. Early veliger, 4 days, dorsal view. 3. Veliger, 7 days, ventral view. 4. Veliger, 12 days, lateral view. 5. Veliger, newly hatched.

beginnings of coiling are visible (Text-fig. 3). Growth and development, however, continue for a further five days before hatching, the shell becoming brown-pigmented and distinctly coiled, with a widely flared aperture, the larval heart conspicuous and active and the yolk reserves of the embryo almost completely resorbed (Text-fig. 4). Withdrawal into the shell also becomes possible during this time.

On hatching from its envelope, the veliger makes its way to the surface of the jelly and escapes into the surrounding water. The velar lobes, each of which has a black-pigmented dorso-lateral margin, spread out, the velar cilia begin to beat rapidly and the veliger swims immediately to the water surface (Text-fig. 5). Pelagic plankto-

trophic life is maintained for at least four days. Attempts to keep the veligers alive beyond this time and follow their metamorphosis have so far proved unsuccessful, but it seems likely that pelagic life is of several weeks' duration.

The rate of development outlined above is typical of eggs at the periphery of the jelly mass. Eggs in the interior of the mass develop more slowly, so that veligers continue to escape from the jelly for several days.

Discussion.

B. nanum thus follows early development within the protection of a gelatinous spawn by escape as a pelagic planktotrophic veliger. In this it resembles the Atlantic species of similar habitat, *Lacuna divaricata* (Hertling and Ankel, 1927; Hertling, 1928; Lebour, 1937; Thorson, 1946) and *Littorina littorea* (Hayes, 1929; Linke, 1934; Lebour, 1937; Moore, 1937; Thorson, 1946), save that the latter lays its eggs in floating capsules.

Of the species which replaces *B. nanum* in the upper littoral, *Melaraphe unifasciata*, we have at present no direct knowledge of the life history. The corresponding Atlantic species, *Littorina obtusa*, which has a gelatinous spawn, and *L. saxatilis*, which is ovioviviparous, hatch at the crawling stage (Pelseneer, 1911; Delsman, 1914; Linke, 1934; Thorson, 1946). Intensive searching of the habitat of the Harbord population of *M. unifasciata* at a time (November-January) when the females contain ripe yellow ova has failed to yield corresponding egg masses, and no animals have yet been found to contain developing embryos. It seems probable that *M. unifasciata* resembles the supra-littoral Atlantic species *Littorina neritoides* (Lebour, 1935), laying its eggs in floating capsules and hatching as a planktotrophic veliger, especially as recent work by Habe (1956) and Kojima (1958) has revealed an identical mode of spawning for *Nodilittorina pyramidalis*, whose supra-littoral distribution overlaps that of *M. unifasciata*. The curious anomaly of adaptation to extreme exposure and retention of planktotrophic early development thus appears to be especially marked in New South Wales rock-platform littorinids.

The present study of *B. nanum* also supplements the work of H. Anderson (1958) on spawning and development in *B. melanostoma* and *B. auratum*. The former, in contrast to *B. nanum*, shows adaptation to prolonged exposure by spawning fewer and larger eggs in jelly masses from which the young hatch at the crawling stage (compare *Littorina obtusata*). In *B. auratum*, however, although the habitat extends to the supra-littoral of mangrove swamps, the egg masses resemble those of *B. nanum* and the embryos probably hatch as planktotrophic veligers. This further example of retention of planktotrophic development in a supra-littoral species finds a parallel in the ovioviviparous supra-littoral mangrove species of Bermuda and Florida, *Littorina angulifera*, in which the young are released either as free eggs or as planktotrophic veligers (Lebour, 1945; Lenderking, 1954).

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EXPLANATION OF PLATE VIII.

1. *B. nanum*: Female and spawn. × 3.
2. *B. nanum*: Jelly masses containing eggs at a late cleavage stage. × 40.